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Upper Paleolithic Animal Exploitation in the Armenian Highlands: The Zooarchaeology of Aghitu-3 Cave

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Keywords

Armenia, Late Pleistocene, subsistence strategies, ungulates, tooth wear analysis, birds

Abstract

Excavated from 2009-2019 by the Tübingen-Armenian Paleolithic Project, Aghitu-3 Cave is the only stratified Upper Paleolithic site in Armenia. Sedimentary deposits range from 39,000 to 24,000 calibrated years before present (ka cal BP). The main Paleolithic occupations occurred during the accumulation of Archaeological Horizon (AH) VI between 36 and 32 ka cal BP and AH III between 29 and 24 ka cal BP. AH VI was deposited under warm and humid conditions, while AH III shows evidence for cooler and drier conditions. Here we report the results of a comprehensive zooarchaeological study aimed at characterizing early modern human hunting behavior in the Armenian Highlands. Our results indicate a focus on adult goats and equids. Bird remains are present, but we found no evidence of human exploitation. Carcass transport strategies appear more selective than those inferred for other assemblages in the region, suggesting that foragers at Aghitu-3 were exploiting larger hunting territories. Finally, we present the results of a pilot microwear and mesowear study on caprine teeth. The latter found evidence for a highly abrasive grazing diet, which in turn suggests that occupation during the formation of AH III took place in spring or summer.

1 Introduction

The so-called Trans-Caucasian corridor is one of the areas that enabled hominin dispersal out of the Levant and into the rest of Eurasia during the Pleistocene (Bar-Yosef and Belfer-Cohen, 2001; Fernández Jalvo et al., 2010). Early paleoanthropological evidence associated with this route of dispersal includes the Dmanisi (Georgia) fossil hominins 1.8 million years ago (Gabunia et al., 2000) and the easternmost occurrence of

Homo heidelbergensis at Azokh Cave (Nagorno-Karabagh) between 400-250 thousand years before present (ka BP) (Kasimova, 2001; King et al., 2016). Later, between Marine Isotope Stage 5-3 (ca. 125-30 ka BP), glacial oscillations turned the Greater Caucasus into a biogeographic barrier (e.g. Seddon et al., 2002). Middle Paleolithic hominins – positively identified as Neanderthals in the region (Pinhasi et al., 2012) – probably could not cross this mountain range, as evidenced by the technological differentiation of groups north and south of the Greater Caucasus (Hublin, 2002; Adler and Tushabramishvili, 2004; Meignen and Tushabramishvili, 2010). Anatomically Modern Humans (AMH) producing Upper Paleolithic material culture (Nioradze and Otte, 2000; Tushabramishvili et al., 2011; Margherita et al., 2017) arrived in the Southern Caucasus after the local disappearance of Neanderthals (Adler et al., 2006; Pinhasi et al., 2012; Pleurdeau et al., 2016). Importantly, technological similarities between Upper Paleolithic assemblages on both sides of the Greater Caucasus suggest that AMH did cross the mountain range (Pleurdeau et al., 2016). Characterizing the differences, if any, between the subsistence strategies of Neanderthals and AMH is crucial to understand if the disappearance of the former and the colonization by the latter can be attributed to economic decisions *sensu stricto* versus social and demographic processes (cf. Adler et al., 2006).

The available zooarchaeological evidence suggests that Middle and Upper Paleolithic foragers on both sides of the Caucasus hunted prime aged medium (caprine) and large (bovine) ungulates, in varying proportions depending on seasonality and hunting territory (Bar-Oz and Adler, 2005; Adler et al., 2006; Cleghorn, 2006; Bar-Oz et al., 2008; Yeshurun et al., 2014; Pleurdeau et al., 2016; Bălăşescu et al., 2017). In these assemblages both the proportion of carnivores and the overall taxonomic richness are low (Bar-Oz et al., 2012). At Hovk-1 Cave in Armenia (2040 m above sea level [asl]), the Late Pleistocene faunal assemblage, which is largely non-anthropogenic, is characterized by a higher proportion of red deer (*Cervus elaphus*) compared to anthropogenic assemblages (Bar-Oz et al., 2012). This suggests that Middle and Upper Paleolithic foragers exploited preferentially more open environments and only secondarily forested areas. Importantly, this picture implies overall continuity in the subsistence strategies of Neanderthals and AMH, without the increase in diet breadth observed at Mediterranean sites (Stiner, 2001).

Most of the available Late Pleistocene zooarchaeological data for the southern Caucasus comes from a handful of thoroughly studied and published assemblages from the Imereti Region of the Republic of Georgia. Sites include Middle and Upper Paleolithic Ortvale Klde (in particular the 43-42 ka cal BP Middle Paleolithic assemblage; Bar-Oz and Adler, 2005; Adler et al., 2008), Upper Paleolithic Dzudzuana Cave (beginning at 34.5 ka cal BP; Bar-Oz et al., 2008; Bar-Yosef et al., 2011) and Upper Paleolithic Bondi Cave (40-27 ka cal BP; Yeshurun et al., 2014; Pleurdeau et al., 2016). Analogous information is available for the much younger Epigravettian assemblage from Kalavan-1 in Armenia dated to 16 ka cal BP (Montoya et al., 2013; Tornero et al., 2016; Bălăşescu et al., 2017). Tooth eruption and replacement patterns from Ortvale Klde (530 m asl) suggests occupations during late fall and/or early spring which targeted migrating Caucasian tur (*Capra caucasica*), while during the summer, this species would have been present at higher elevations (Adler et al., 2006). Similarly, seasonal occupations at the end of summer or in autumn are suggested at Kalavan-1 (1640 m asl), where foragers targeted migrating mouflon (*Ovis orientalis*) (Tornero et al., 2016; Bălăşescu et al., 2017). At Dzudzuana Cave (560 m asl) in Unit D (34.5-32.2 ka cal BP) Caucasian tur is the main species, which suggests occupation in late autumn or winter, when the herds descended from higher elevations. However, the sample from this unit is quite small. In Unit C (27-24 ka cal BP) steppe bison (*Bison priscus*) is the main species, which may indicate occupation in spring or summer, when the herds ascended the hills (Bar-Oz et al., 2008; Bar-Yosef et al., 2011). A diachronic change in the relative representation of tur and bison is also attested within the Upper Paleolithic at Bondi (477 m asl) (Yeshurun et al., 2014).

The data summarized above point at brief seasonal occupations along the migratory paths of tur and bison. Most sites in the southern Caucasus and in the Armenian Highlands are located at higher elevations and

dominate our view of Middle and Upper Paleolithic subsistence. There is paucity of assemblages from lower elevations. An interesting case is that of Satsurblia in western Georgia (300 m asl), with deposits accumulated before and after the Last Glacial Maximum (25.5-24.5 and 17.9-16.2 ka cal BP, respectively; Pinhasi et al., 2014). The assemblage is dominated by red deer and wild boar (*Sus scrofa*) and indicates the exploitation of forested environments (Pinhasi et al., 2014). Only a small portion of the fauna from this site has been published to date and accompanying taphonomic information is limited, but hopefully this assemblage will add important insights to our understanding of Paleolithic lifeways once it is fully reported.

Very limited information is available on other faunal assemblages from the Lesser Caucasus. At Azokh (962 m asl) Beds IV and III (Middle Pleistocene) cut marked fauna is associated with Middle Paleolithic stone tools (Fernández Jalvo et al., 2010; Marin-Monfort et al., 2016). Early Middle Paleolithic faunal assemblages are known from Djruchula Cave (600 m asl) in the Imereti Region (Layer 2: 210-260 ka BP; Layer 1: ca. 140 ka BP; Adler and Tushabramishvili, 2004; Mercier et al., 2010), but have not been published. Late Pleistocene zooarchaeological assemblages from the Imereti Region include a fauna dominated by *Bison* from Bronze Cave (>46 ka cal BP; Adler and Tushabramishvili, 2004; Rivals and Arellano, 2010; Pinhasi et al., 2012), abundant *Ursus spelaeus* among the remains of other species at Undo Cave (Moncel et al., 2015: 111) and several others (Gvardjilas Klde, Samertskhle Klde, Dewiss Chwreli, Ortvala, Sakajia; Nioradze and Otte, 2000; Rivals and Arellano, 2010; Pinhasi et al., 2012; and references therein). In Armenia, a small Middle Paleolithic faunal assemblage from Kalavan-2 (1630 m asl) has been described (Ghukasyan et al., 2010).

In this paper we contribute to the understanding of Paleolithic subsistence in the Armenian Highlands and neighboring regions by reporting the results of a comprehensive study of the zooarchaeological assemblage of Aghitu-3 Cave in southern Armenia. This cave is currently the only stratified Upper Paleolithic site in Armenia and therefore our results complement, but do not simply replicate, results from the environmentally distinct Imereti region. Specifically, we test whether previous paleoenvironmental reconstructions are supported by the results of our analyses and whether the subsistence strategies attested at Aghitu-3 are consistent with those attested at other sites south of the Greater Caucasus.

2 Background

Aghitu-3 Cave is located in the Syunik Province of southern Armenia at an elevation of 1601 m asl (Figure 1 andFigure 2). The joint research team headed by B. Gasparyan of the Armenian National Academy of Sciences and A. Kandel of the Heidelberg Academy of Sciences and Humanities conducted excavations every summer between 2009-2013, in 2015 (Kandel et al., 2017) and again in 2016-2019, with new field seasons ongoing. The excavations revealed evidence of Upper Paleolithic occupation within the dripline of the cave. On the large terrace in front of the cave, an intact tomb containing seven individuals and several linear stone structures provided evidence for Late Hellenistic occupation dating to the 1st century BC. Based on excavated materials, it is clear that people also used the cave during the Bronze Age, Iron Age and medieval periods (Kandel et al., 2011). In 2016-2019 excavation has focused on the Late Hellenistic and Iron Age occupations of the site.

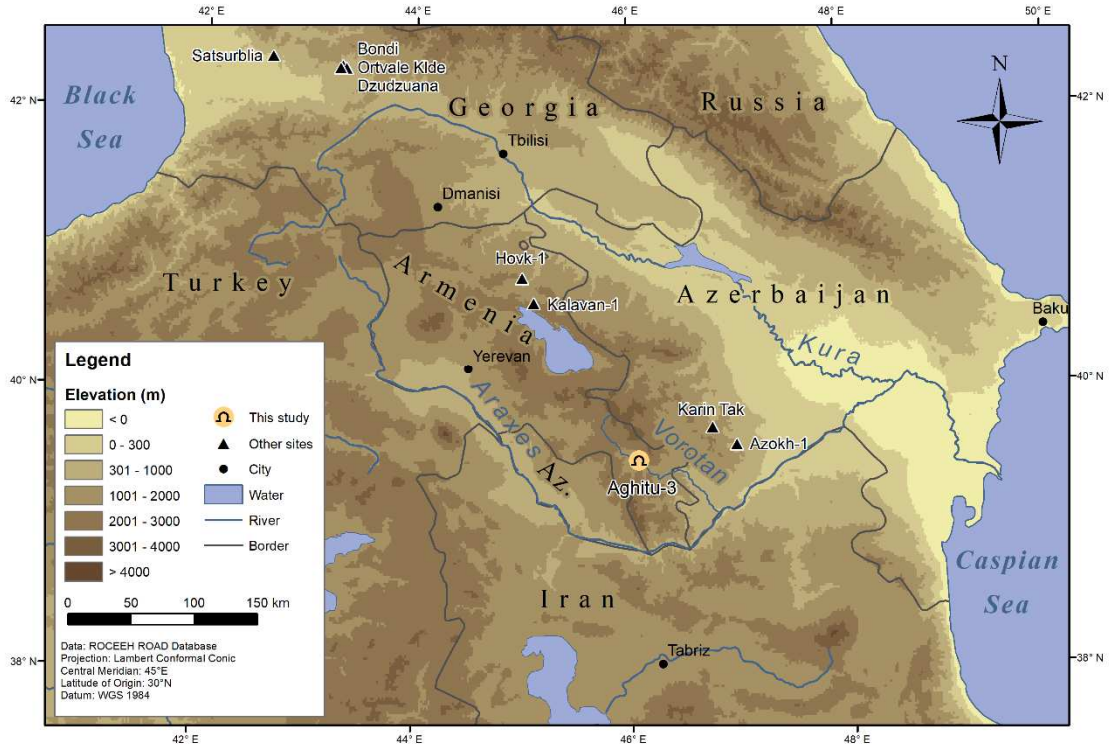

Figure 1 – Map showing the location of Aghitu-3 Cave and the main sites mentioned in the text. (Map: C. Sommer)

Figure 2 - Aerial view of Aghitu-3 Cave taken with a drone in the autumn of 2017. The Paleolithic excavation is located within the dripline of the cave, while the Late Hellenistic excavation is on the terrace in front of it. (Photo: S. Aghaian)

Aghitu-3 Cave documents several phases of Paleolithic occupation between 39-24 ka cal BP. The deepest layer of the sequence is Archaeological Horizon (AH) VII and provides the first evidence for modern human

behavior in Armenia, based on its laminar stone technology. Settlement during this warm and humid climatic phase was sparse as shown by occasional stone artifacts, bones and charcoal fragments. People used two reduction sequences to knap stone artifacts. The first involved the use of large, single platform, bidirectional cores to produce large blades (≥10 mm in width), and the other used small, single platform, unidirectional cores to create thin bladelets (<10 mm in width). The deposition of overlaying AH VI began about 36 ka cal BP as climatic conditions remained warm and humid. A slight increase in the intensity of settlement is evident through the presence of small, intact combustion features containing charcoal, ash and rubified sediment surrounded by scatters of stone artifacts. People knapped mostly bladelets from small unidirectional cores. Beginning about 32 ka cal BP, AHs V and IV document increasingly colder and drier conditions, during which time occupation of the cave almost ceased, based on the presence of very few finds. We consider both layers to be archaeologically sterile. About 29-24 ka cal BP, occupation intensity increased dramatically in AH III, as people repeatedly returned to the site during a cold and dry period leading into the Last Glacial Maximum. In AH III, dense layers of cultural material include many stone artifacts, numerous faunal remains, bone tools and shell beads. Combustion features consist of approximately continuous ashy deposits containing much charcoal and numerous finds.

R. Ghukasyan presented the results of his preliminary analysis of 2291 large mammal specimens from AH VII-III in a previous paper (Kandel et al., 2017). In the same publication, B. Gruwier identified 261 avian specimens from the same layers. Through expanded sorting efforts and a reanalysis of the original collection, we now provide a more detailed report of the large mammal (n = 2577) and avian assemblages (n = 332) as well as the results of a pilot study to examine microwear and mesowear on herbivore teeth.

3 Materials and methods

3.1 Large mammals

The large mammal remains from AH VII-III were studied at the Institute for Scientific Archaeology of the University of Tübingen, Germany. The assemblage from Aghitu-3 includes piece-plotted bones ≥20 mm in maximum dimension as well as smaller bones <20 mm in maximum dimension that could be identified at least to skeletal element. The latter come from known volumes of sediments whose provenience is also recorded with spatial coordinates and which were dry screened through 5 and 2 mm sieves (Kandel et al., 2017). This sampling strategy ensures comparability with experimentally produced and naturalistic faunal assemblages (Marean et al., 2000: 215). We note that in this study, we opted for a more cautious approach in identifying the large mammal remains, so that some differences exist compared with the work published in Kandel et al. (2017.)

We used a Microsoft Access database with tailored data masks to enter data. Each specimen is associated with a unique numeric identifier. Basic descriptive data include taxon, element, portion of element, side, age (epiphyseal fusion or tooth eruption and wear stage), completeness and weight. The reference osteological collection of the Institute for Scientific Archaeology of the University of Tübingen was used for comparison. When the taxonomic identity of a specimen could not be determined at least to the genus level, the specimen was assigned to a size-class as follows: size 1 (fox/hare size), size 2 (sheep/goat size), size 3 (horse size), size 4 (bison/aurochs size). Given the expected composition of the faunal community, it is likely that size 2, 3 and 4 specimens represent in fact caprines, equids and large bovines, respectively. Sorting sheep from goats in archaeofaunal assemblages is particularly challenging. Blind testing of commonly used criteria to distinguish mandibles and mandibular teeth of sheep and goat has shown high rates of misidentification (Zeder and Pilaar, 2010). Therefore, in this analysis we limit species-level identifications of caprines to the postcranium and only to those features that have shown low rates of misidentification after blind testing (Zeder and Lapham, 2010). The identification of equids to species is also

a complicated matter. In the Armenian Highlands either or both horse (*Equus ferus*) and onager (*Equus hemionus*) could be present. Even though both taxa suggest an open landscape, the distinction is relevant because modern representatives of these species have different ecological preferences. Wild horses prefer productive patches such as riparian habitats, while onagers range more widely and exploit low-quality pastures (Kaczensky et al., 2008). Identification of these species using occlusal enamel folding patterns is inconsistent across analysts (Twiss et al., 2017) and aDNA metabarcoding of Late Pleistocene equid fossils at nearby Karin Tak could not resolve the identification beyond the genus level (Antonosyan et al., 2019). Therefore, we decided to identify equid remains as *Equus sp.*, while acknowledging that if larger assemblages become available size-based groupings may be attempted (cf. Arbuckle and Öztan, 2018).

Fragmentation patterns are informative of the degree of nutritive (fresh) and non-nutritive (dry) breakage of the faunal assemblage (Marean et al., 2000). Here we used the method of Villa and Mahieu (1991), which considers fracture outline and angle of the long bones. Oblique angles and curved outlines are more common in assemblages broken when fresh, while right angles and transverse outlines are associated with dry breakage. Burning is recorded after Stiner et al. (1995). The occurrence of exfoliation, gastric etching, root marks, rodent gnawing, trampling and oxide staining was also noted (Behrensmeyer, 1978; Andrews, 1990; Fisher, 1995). Each specimen was examined with a 10x hand lens under incident light for bone surface modifications. Tooth marks, cut marks and percussion marks were identified following the criteria of Blumenschine et al. (1996). Tooth marks were further qualified as pits, punctures or scores (after Binford, 1981) and the length (for pits and punctures) or mean width (for scores) was measured with digital calipers. The orientation (parallel, transverse or oblique to the longitudinal axis of the bone) and length of cut marks was recorded. Inferences of butchery activity from placement of cut marks are based on Binford (1981) and Nilssen (2000). Other forms of anthropogenic modification were also noted and include: peeling and end-bending on ribs (White, 1992; Saladié et al., 2013a), longitudinal cracks and crushing possibly caused by biting (Binford, 1981), as well as suspected projectile impact marks (O'Driscoll and Thompson, 2014; Duches et al., 2016).

The basic counting unit used in this study is the Number of Identified Specimens (NISP), which tallies all specimens identified at least to element type (e.g. long bone) and size class. Specimens that include diagnostic features and could be identified to exact element are used to calculate the Minimum Number of Elements (MNE; Lyman, 2008). The MNE is then divided by the times a certain element occurs in a complete skeleton, either taking into account the side or not, to calculate the Minimum Number of Individuals (MNI) and the Minimum Animal Units (MAU), respectively (Binford, 1978; Lyman, 2008). We also calculated the MAU of specific portions of elements for which experimental bone mineral density values are available (values for equids from Lam et al. (1999), values for caprines from Lyman (1994)). We then calculated the %survivorship of these portions (equivalent to %MAU, i.e. (MAU/highest MAU)*100; Binford, 1978; Lyman, 1994) and tested it for correlation with bone mineral density. If they correlate, the less dense elements and portions of elements have been obliterated by post-depositional processes, which needs to be considered in the interpretation (Lyman, 1994). Density-mediated attrition is the expected outcome of several post-depositional processes, carnivore ravaging being of particular importance in many archaeological contexts (Marean and Spencer, 1991; Blumenschine and Marean, 1993), although other abiotic processes can subsequently reduce the identifiability of the denser portions as well (Conard et al., 2008).

The relative representation of different skeletal elements (expressed as %MAU) can be compared with measures of food utility of those elements to investigate carcass transport decisions. For equid, we use the General Utility Index for whole bones developed by Outram and Rowley-Conwy (1998). For caprines, we use the Standardized Food Utility Index for whole bones of Metcalfe and Jones (1988). The latter was calculated for reindeer from the Modified General Utility Index of Binford (1978). However, since the

Modified General Utility Index for reindeer correlates well with that determined for sheep, the use of the reindeer Standardized Food Utility Index for caprines is justified (cf. Marean and Frey, 1997: 704). As density-mediated attrition can confound the behavioral signal of transport, the correlation of %MAU and utility indices is calculated separately for the low-survival and high-survival elements, the latter including long bones, the mandible and the cranium (Marean and Frey, 1997; Marean and Cleghorn, 2003; Yeshurun et al., 2007; Schoville and Otárola-Castillo, 2014; Faith and Thompson, 2018).

3.2 Tooth wear analysis

Tooth mesowear analysis is a method of categorizing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices in ways that are correlated with the level of abrasiveness in the diet (Fortelius and Solounias, 2000). Mesowear was scored macroscopically from the buccal side of upper molars and lingual side of lower molars. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices were omitted from mesowear analysis (Rivals et al., 2007). In this study, the standardized method introduced by Mihlbachler et al. (2011) was employed. The method is based on seven cusp categories (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). The average value of the mesowear data from a single sample of fossil dentition corresponds to the "mesowear score".

Tooth microwear patterns were analysed using the light stereomicroscope technique established by Solounias and Semprebon (2002). The microwear was quantified through direct observation on a 0.16 mm^2 area following Solounias and Semprebon (2002). The numbers of pits and scratches were quantified in two areas of each tooth and then averaged. Other variables were qualitatively scored: presence/absence of large pits, gouges (i.e. circular features with irregular shape), cross scratches (i.e. scratches oriented differently than the majority of the scratches), hyper-coarse scratches (i.e. very large scratches), and puncture pits. The variability of the microwear pattern is used to estimate the seasonality of the occupation(s) following Rivals et al. (2015).

3.3 Avian fauna

Most of the bird remains were recovered during the picking of fine sediments. The avian fauna was identified using the comparative collections of the Charles-de-Gaulle University – Lille III, France, and the Natural History Museum of Rotterdam, the Netherlands. In addition, a number of relevant keys and atlases were used including Bacher (1967) and Woelfle (1967) for the Anseriformes, Ebersdobler (1968) and Kraft (1972) for the Galliformes, Langer (1980) for the Strigiformes, and Otto (1981) and Schmidt-Burger (1982) for the Falconiformes. Specimens were measured using the standard methods developed by von den Driesch (1976) to aid with the identifications. Each bone was systematically examined for traces of human modification as well as for traces potentially informative about the taphonomic history of the assemblages.

4 Results

4.1 Large mammals

The current sample of large mammals from AH III and below includes 2577 specimens (Table 1). Specimens from AH II, AH I and the surface are excluded from the analysis because they come from disturbed contexts. Nonetheless, we draw special attention to a partial proximal phalanx of a medium-sized felid from AH I, tentatively identified as leopard (*cf. Panthera pardus*). This species is rare in archaeological assemblages, but securely attested in the Late Pleistocene (Antonosyan et al., 2019). Leopard is critically endangered in Armenia today (Khorozyan et al., 2010), so its presence is worth mentioning although an exact age for this specimen is not available. Of the caprine specimens from AH III and below, only 13 could be identified to genus, and these were all assigned to *Capra.* No *Ovis* remains were encountered.

Therefore, it seems likely that most of the specimens assigned to *Ovis/Capra* can reasonably be attributed to wild goats. Although efforts at refitting were not systematically undertaken, five refit sets were noted during data collection (three from AH III, two from AH VI). None of these refit across AHs, which supports the integrity of the deposits, along with field observations, dating results and sedimentology. Of special note is a fragmentary right metacarpal of a caprine from AH III, whose surface is altered by dendritic etching, which bears scars that we interpret as evidence of its use as a bone retoucher (Figure 3). To our knowledge this is the first such implement described from the region.

Taxon	**AH III**	**AH IV**	**AH V**	**AH VI**	**AH VII**
Bos/Bison	20	-	-	4	1
Equus sp.	354	-	-	9	11
Cervus elaphus	17	-	-	1	1
Capra sp.	10	1	-	2	-
Ovis/Capra	413	2	8	158	47
Lepus sp.	27	4	-	31	9
Canis lupus	1	1	2	5	1
Vulpes sp.	1	-	-	-	2
Size class 1	14	1	1	10	1
Size class 2	617	7	9	189	47
Size class 3	371	7	3	20	14
Size class 4	40	-	-	3	1
Indeterminate	70	-	-	7	2
TOTAL	1955	23	23	439	137

Table 1 – Identification of large mammals from Archaeological Horizons VII–III of Aghitu-3.

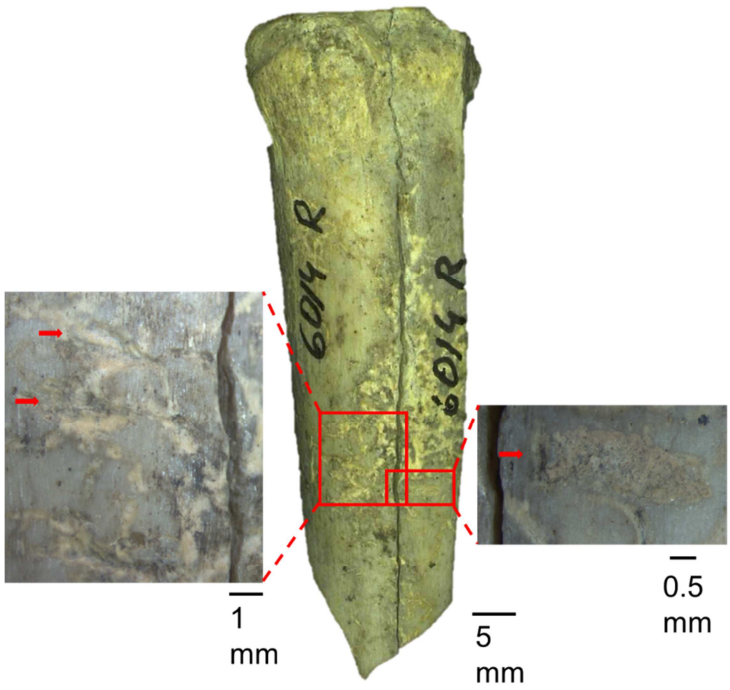

Figure 3 – Bone retoucher on a right metacarpal of a caprine (I12-187, AH III), with details of the working areas.

The analyses presented here focus mainly on the largest samples, which come from AHs III and VI. Both layers are dominated by caprines, whereas only AH III yielded abundant equid remains. This is consistent

with a more open habitat and cool and dry conditions associated with the formation of this deposit (Kandel et al., 2017). AH IV yielded a small sample including a fetal distal humerus of a canid. AH V also yielded an equally small sample including the distal humerus of a juvenile canid and the complete skull of an adult canid. The latter features five large punctures on the cranium and several cut marks on the buccal side of the left hemimandible, suggesting both human and carnivore interaction with the skull (Loog et al., 2019). The presence of immature carnivore remains is sometimes associated with den assemblages, but the number of carnivore specimens remains too low to draw such a conclusion (cf. Stiner, 1991).

Table 2 summarizes the fracture patterns observed on size 2 and 3 long bones (see also Supplementary Online Material (SOM)). Marean et al. (2000) conducted experiments with fresh assemblages of size 1 and 2 bovids fragmented by: i) hammerstones; ii) carnivores; and iii) hammerstones followed by carnivores. They observed that the proportions of shaft fragments displaying right angles and transverse outlines were below 4.5% and 10.5%, respectively. At Aghitu-3 the proportions of right and transverse breaks are close to or below these thresholds, indicating that the assemblage was fragmented while it still held nutritional value and did not subsequently undergo substantial post-depositional breakage (Table 3).

		Size 2			**Size 3**		
Angle	**Layer**	**Oblique**	**Intermediate**	**Right**	**Oblique**	**Intermediate**	**Right**
	AH III	342	17	22	214	21	17
	AH VI	62	2	1	11	-	-
Outline		**Curved**	**Intermediate**	**Transverse**	**Curved**	**Intermediate**	**Transverse**
	AH III	354	18	9	228	12	12
	AH VI	61	4	-	11	-	-

Table 2 – Number of long bone fragments exhibiting different fracture characteristics.

Layer	**% right breaks**	**% transverse outlines**
AH III Size 2	5.8	2.4
AH III Size 3	6.8	4.8
AH VI Size 2	1.6	-
AH VI Size 3	-	-

Table 3 – Proportions of long bone fragments displaying dry break characteristics.

Table 4 reports counts of specimens by burn color code (after Stiner et al., 1995). AH III is the only deposit with abundant traces of bone burning (n = 99, i.e. 5.1% of the bones in AH III. Size 1: n = 1, Size 2: n = 56; Size 3: n = 30). AHs IV and V bore no burnt bones, consistent with them being archaeologically sterile (Kandel et al., 2017). AH VI yielded only two burnt bones: the proximal portion of a rib and an indeterminate fragment, both completely charred. AH VII yielded a single burnt bone: a calcined complete second phalanx of a canid.

Layer	**0**	**1**	**2**	**3**	**4**	**5**	**6**
AH III	1856	29	23	36	3	1	7
AH IV	-	-	-	-	-	-	-
AH V	-	-	-	-	-	-	-
AH VI	437	-	-	2	-	-	-
AH VII	137	-	-	-	-	-	1

Table 4 – Specimen counts by burn color code (after Stiner et al., 1995). 0 = unburnt, 1-3= black/charred (<50%, >50%, 100%, respectively), 4-6 white/calcined (<50%, >50%, 100%, respectively). When more than one color occurs, the highest value is recorded.

Table 5 reports counts of specimens bearing various bone alterations. Loss of the cortical surface is rare, occurring on 1.3% of the specimens in AH III. Gastric etching occurs on 1.2% and 17.8% of the bones in AHs III and VI, respectively. Of the 110 specimens with traces of gastric etching, only seven belong to size 1 animals (AH III: n = 1; AH V: n = 1; AH VI: n = 4; AH VII: n = 1). In one of these cases, etching co-occurs with a carnivore tooth pit. Therefore, non-human accumulation of large mammals can mostly be attributed to mammalian carnivores, rather than birds of prey. Black oxide staining is very frequent in all layers (AH III: 69%; AH IV: 87%; AH V: 74%; AH VI: 69%; AH VII: 71%).

Layer	**EX**	**E**	**G**	**RM**	**T**	**O**
AH III	26	23	2	63	5	1353
AH IV	-	1	-	6	-	20
AH V	-	4	-	1	-	17
AH VI	2	78	1	55	1	302
AH VII	2	4	-	18	-	97

Table 5 – Counts of specimens bearing various bone alterations. EX = Exfoliation and loss of the cortical surface; E = Gastric etching; G = Rodent gnawing; RM = Root marks; T = Trampling; O = Oxide staining.

Table 6 reports counts of diaphyseal specimens bearing bone surface modifications. The analysis is limited to diaphyseal specimens >20 mm with a medullary cavity and lacking trabecular bone because experimental observations have shown that this category of fragments is the most informative to identify agents of accumulation (e.g. Marean et al., 2000). For tallies of bone surface modifications including all skeletal elements and portions see the SOM. AH III is the only deposit to provide a large enough sample of bone surface modifications for further discussion. The ratios of specimens bearing a percussion mark relative to specimens bearing a tooth mark (PM/(PM+TM); Thompson et al., 2017) are 0.61 and 0.81 for sizes 2 and 3, respectively. These values suggest that the assemblage was primarily accumulated by humans, whereas carnivores either ravaged the refuse or primarily accumulated a marginal amount of bone (cf. Thompson et al., 2017: table 3). Experiments in which carnivores ravaged assemblages broken with hammerstones, without accumulating additional bones, found that about 5% of the long bone fragments bore both a percussion mark and a tooth mark (Capaldo, 1995; Marean et al., 2000). At Aghitu-3 such overlaps occur only three times in AH III (Size 2: n = 1; Size 3: n = 2; i.e. <1%) and once in AH VI (Size 2). Therefore, it is likely that carnivores independently accumulated a portion of the assemblage in AH III.

Layer	**Size**	**N**	**CM**	**PM**	**TM**
AH III	1	13	-	-	-
	2	399	42	37	24
	3	272	25	41	11
	4	6	-	-	-
AH VI	1	23	1	-	3
	2	32	3	3	5
	3	10	1	2	-
	4	3	-	-	-
AH VII	1	3	-	-	1
	2	47	-	1	1
	3	11	1	-	-
	4	-	-	-	-

*Table 6 – Counts of diaphyseal specimens bearing bone surface modifications. CM = cut mark; PM = percussion mark; TM = tooth mark. AHs with no specimens bearing bone surface modifications are not shown. All counts are fragment-counts (*sensu *Abe et al., 2002).*

We measured 204 tooth marks (pits, punctures, scores) (Table 7, raw data in the SOM). Experimental observations (Selvaggio, 1994; Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Andrés

et al., 2012) have shown that tooth mark size varies according to the size and bite strength of the predator, but also by bone tissue (compact or cancellous), although researchers disagree about which tissue retains the most informative marks. Importantly, there is overlap across carnivores in the dimensional range of tooth marks and the effect of prey and bone size remains unclear. As noted by Andrés et al. (2012), many experimental works deal with very small samples of marks, resulting in broad confidence intervals and therefore much overlap across carnivores. Following their recommendation, in Figure 4 we plot only experimental data for which sample size >30. However, given the limited size of our dataset, we decided to include smaller archaeological sets for comparison. The results indicate that in AH III bones were modified by small canids (e.g. foxes) or perhaps medium felids (e.g. lynxes, leopards), whereas AH VI records the involvement of larger predators, perhaps wolves, which are the only carnivore attested in the archaeofaunal assemblage of Aghitu-3.

Layer	**Prey size**	**Mark type**	**Bone tissue**	**N**	**Range mm**	**Mean mm**	**SD**
AH III	Size 1	Pit	Cancellous	4	0.6-2.5	1.4	0.96
	Size 2	Pit/Puncture	Compact	36	0.3-6.4	1.9	1.34
			Cancellous	30	0.1-6.5	2.2	1.36
		Score	Compact	5	0.5-1.0	0.7	0.27
			Cancellous	4	0.7-1.0	0.9	0.23
	Size 3	Pit	Compact	22	0.3-4.6	1.7	1.05
			Cancellous	22	0.3-4.2	1.6	1.07
		Score	Compact	10	0.6-3.0	1.9	0.66
			Cancellous	19	0.5-1.2	0.8	0.21
	Size 4	Pit	Compact	2	3.2-4.5	3.9	-
AH IV	Size 2	Pit	Cancellous	4	1.0-2.0	1.7	0.46
AH VI	Size 1	Pit/Puncture	Compact	3	0.9-6.1	3	2.7
			Cancellous	1	0.7	-	-
	Size 2	Pit/Puncture	Compact	7	1.0-5.4	3.1	1.73
			Cancellous	17	1.3-7.4	3.7	1.64
		Score	Compact	7	0.4-2.5	0.8	0.77
	Size 3	Pit	Cancellous	3	1.6-2.3	2	0.36
AH VII	Size 1	Pit	Compact	3	2.2-2.2	2.2	0
	Size 2	Pit/Puncture	Compact	2	0.3-0.3	0.3	-
			Cancellous	2	1.2-2.4	1.8	-
	Size 3	Pit	Cancellous	1	3.6	-	-

Table 7 – Summary statistics of the measured tooth marks from Aghitu-3. For pits and punctures, the major axis (length) of the mark is measured. For scores, the average width is reported. SD = standard deviation.

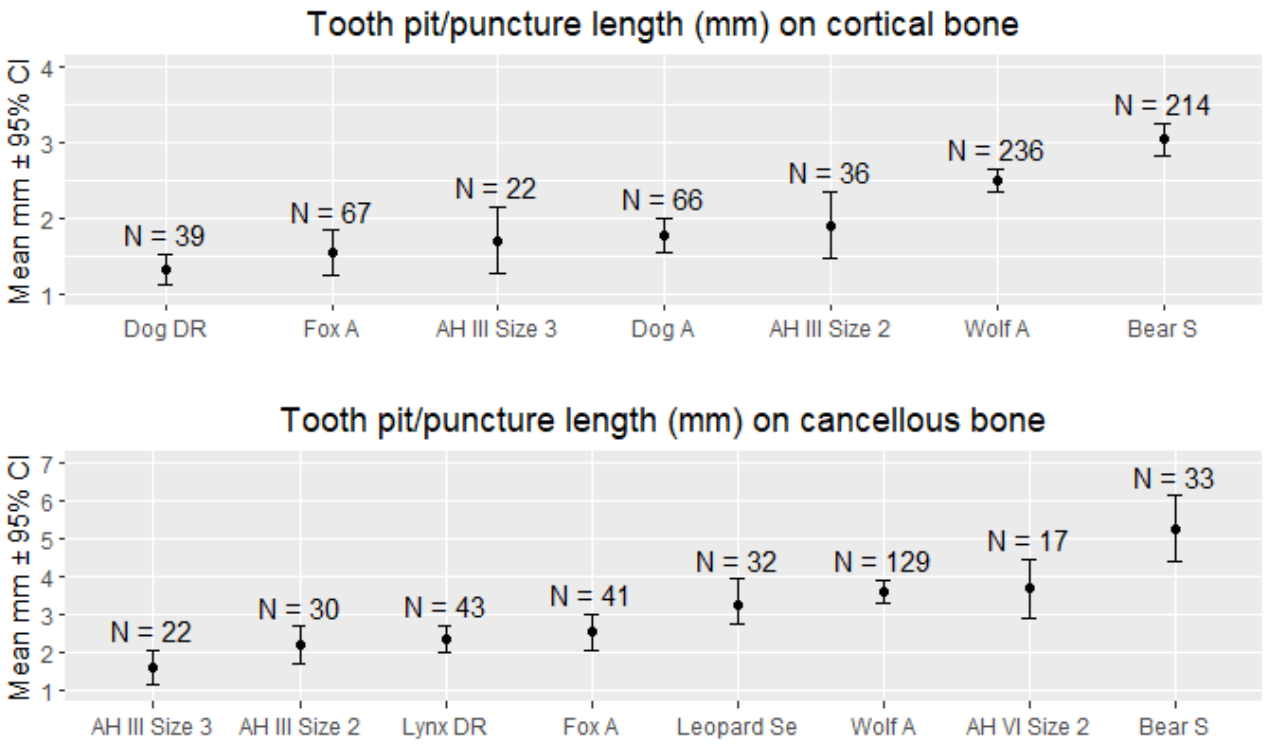

Figure 4– Size of the tooth pits/punctures from Aghitu-3 compared to experimental data. S = Saladié et al. (2013b), A = Andrés et al. (2012), DR = Delaney-Rivera et al. (2009), Se = Selvaggio (1994).

The only carnivore specimen with cut marks is the left hemimandible of a canid from AH V. AH VI yielded the only cut-marked fragment of a size 1 animal (a *Lepus* tibia). In this layer, cuts occur diagonally on midshaft fragments and perpendicularly on a rib of caprine, suggesting defleshing and removal of viscera, respectively. As for size 3 animals, cut marks occur diagonally on a midshaft fragment and transversally on the transverse process on a lumbar vertebra, in both cases suggesting defleshing. In AH VII, a single size 3 midshaft fragment is cut marked, again indicating defleshing.

In AH III, cut-marked diaphyses represent 10.5% and 9.2% of the size 2 and 3 subsets, respectively (Table 6). Table 8 reports the distribution, orientation and length of individual cut marks (Ncut) on meat-bearing long bones (humerus, radio-ulna, femur, tibia) of size 2 and 3 animals, including the epiphyses. Most of the cuts occur on diaphyseal portions, indicating that cutting activities focused on defleshing. The very small proportion of longitudinal cuts in the size 2 sample suggests that the goal of defleshing was the simple removal of muscle mass, rather than the filleting of long stripes of meat for drying and storage (Soulier and Morin, 2016). Conversely, the proportion of longitudinal cuts in the size 3 sample is compatible with the removal of such meat stripes (Soulier and Morin, 2016), although the sample is small. The difference in butchery practices between size classes is also reflected in the orientation of cut marks on unidentified long bone fragments from AH III (Size 2 Ncut = 62, 77% oblique, 23% transverse; Size 3 Ncut = 75, 8% longitudinal, 47% oblique, 45% transverse; see SOM).

AH III		**Size 2**		**Size 3**	
		Ncut	**%**	**Ncut**	**%**
Distribution	Proximal end	1	1.1	-	-
	Proximal diaphysis	17	19.5	14	45.2
	Midshaft	60	69.0	12	38.7
	Distal diaphysis	9	10.3	5	16.1

	Distal end	-	-	-	-
Orientation	Longitudinal	6	6.9	6	19.4
	Oblique	56	64.4	21	67.7
	Transverse	25	28.7	4	12.9
Length	Mean (mm)	2.9	-	3.9	-
	SD	1.71	-	2.29	-
	Range (mm)	1-9	-	1-9	-

Table 8 – Distribution, orientation and length of cutmarks on meat-bearing long bones (humerus, radio-ulna, femur, tibia) of size 2 and 3 animals from AH III. Ncut = number of cut marks, SD = standard deviation.

Tallies of fragments with cut marks, their relative abundance (%NISP cut) and cut mark-counts (Ncut) by element for AH III are reported in the SOM. Evidence for defleshing has already been discussed with reference to long bones and is supported by cut mark placement across the axial skeleton. Additional butchery activities attested in AH III include skinning of size 2 animals (cuts on metapodials), removal of the equid tongue (cuts on a juvenile hyoid;Figure 5) and removal of the viscera on ungulates of all sizes (abundant cuts on ribs; Size 2: n = 43, Ncut = 188; Size 3: n = 34, Ncut = 145; Size 4: n = 4, Ncut = 13).

Figure 5 – Cut marks on a juvenile equid hyoid (H14-231, AH III).

Other anthropogenic modifications are reported in the SOM. Peeling and bending of the ends were observed on 51 rib fragments, 46 of which are from AH III (Size 2: n = 27, Size 3: n = 17, Size 4: n = 2). Radial cracks associated with biting are suspected on two ribs of size 2 animals from AH III. Probable projectile impact marks (drags) are attested on three size 3 specimens (the spine of a thoracic vertebra, the lateral process of a lumbar vertebra and a diaphyseal fragment;Figure 6).

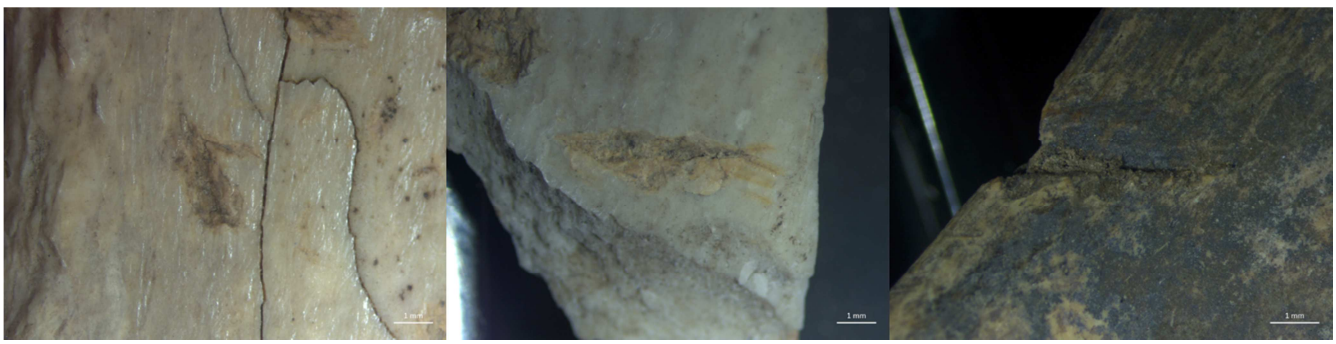

Figure 6 – Probable Projectile Impact Marks on size 3 specimens. Left: spine of a thoracic vertebra (E14-267, AH III); center: diaphysis (E14-296, AH III); right: lateral process of a lumbar vertebra (F12-267, AH III). Scale bars are 1 mm.

Dental ages were determined on eleven specimens from AH III and are reported in the SOM. One equid incisor and one molar fragment of a bovine were attributed to senile animals based on occlusal wear. The remaining nine teeth belong to caprines. Six lower molars come from adult animals (wear stages 8A-15A; Payne, 1973; 1987). An upper premolar is deciduous and two mandibular third molars are also assigned to juveniles because they lack macroscopic wear.

The abundance of different elements (NISP, MNE, MAU, %MAU) for size 2 (AHs III and VI) and 3 (AH III) animals is reported in the SOM and represented in Figure 7. The skeletal element profiles are calculated based on both specimens identified to size and specimens identified to genus. Almost all anatomical portions are represented in each case. Size 2 profiles appear dominated by limb bones, particularly the humerus and the femur, while the latter element is rare among the size 3 elements. The MNI of size 2 animals (caprines) is seven (one juvenile, six adults) in AH III (based on the midshafts of humerus and femur) and six (two juveniles, one subadult, three adults) in AH VI (based on the midshafts of the femur). A seventh individual from AH VI (excluded from tallies of portion survivorship) is a fetus attested by a single distal phalanx. The MNI of size 3 animals (equids) from AH III (based on the midshafts of the tibia and the nutritive foramina of the humerus) is three (one juvenile, two adults).

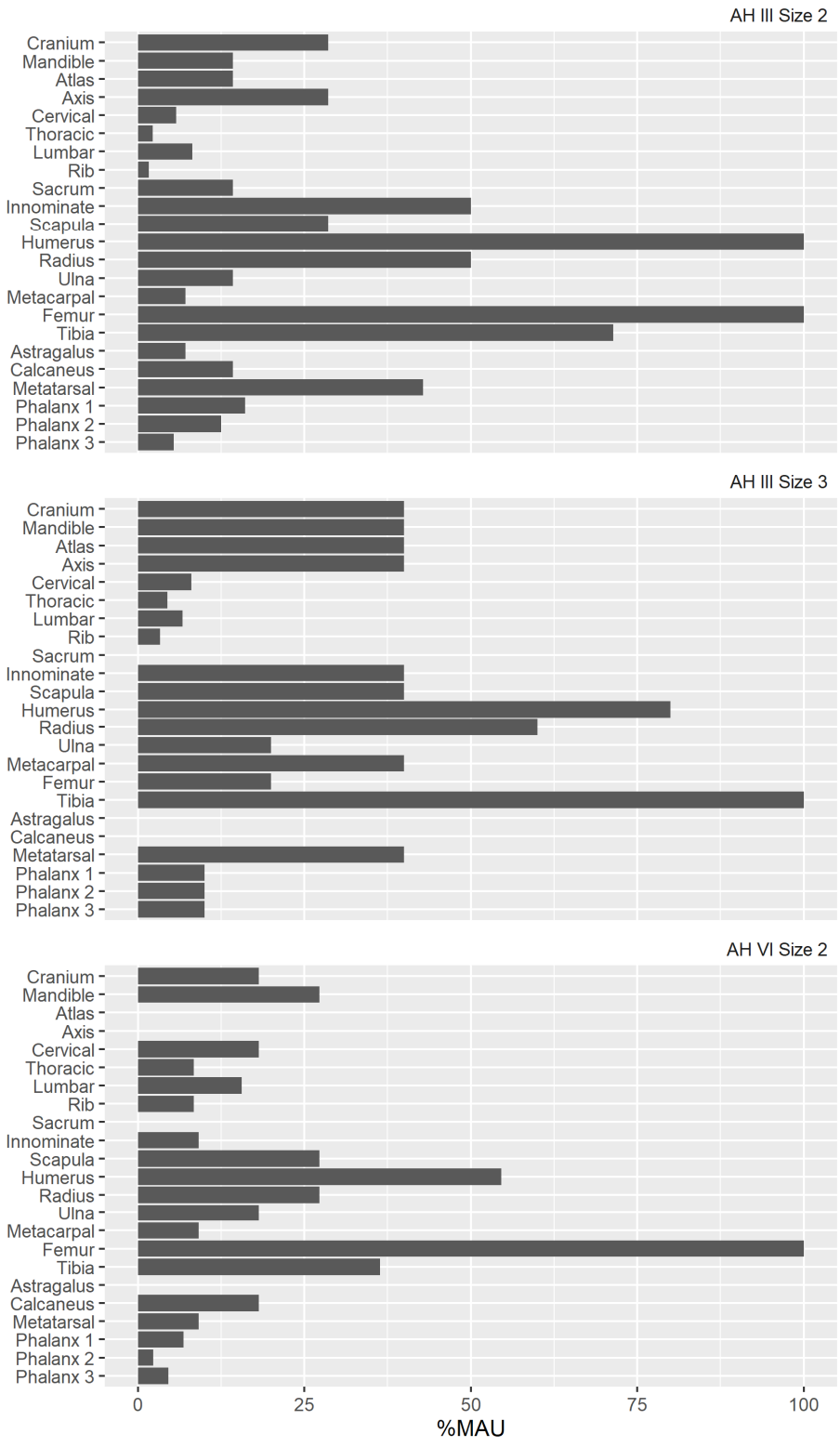

Figure 7 – Skeletal element representation at Aghitu-3.

Survivorship of bone portions (see SOM) and their bone mineral density correlate significantly for caprines (including size 2 specimens) in AH III (Spearman's rho = 0.25, p = 0.034), but not for equids (including size 3 specimens) in AH III (rho = -0.119, p = 0.246) or for caprines in AH VI (rho = 0.059, p = 0.62). This indicates that density-mediated attrition of the bone assemblage at Aghitu-3 was mild at most. Therefore, we can assume that the skeletal element profiles presented above are a reasonably accurate representation of the bones that were transported to the site.

Element nutritional utility and %MAU are plotted in Figure 8 and the correlation coefficients are reported in Table 9. As expected, low survival elements do not correlate with food utility, despite the possibly low incidence of density-mediated attrition at the site. For high survival elements of caprines, %MAU correlate significantly with food utility, indicating that Upper Paleolithic foragers transported carcass portions according to their nutritional value. The correlation between %MAU and food utility for equid high survival elements is negative and non-significant. This is driven by the low representation of the femur, which has the highest nutritional value among the high survival elements. Outram (2006) noted the same phenomenon at other Paleolithic sites and suggested that the femoral "meat roll" may have been frequently separated from the bone before transport because of the high bone weight.

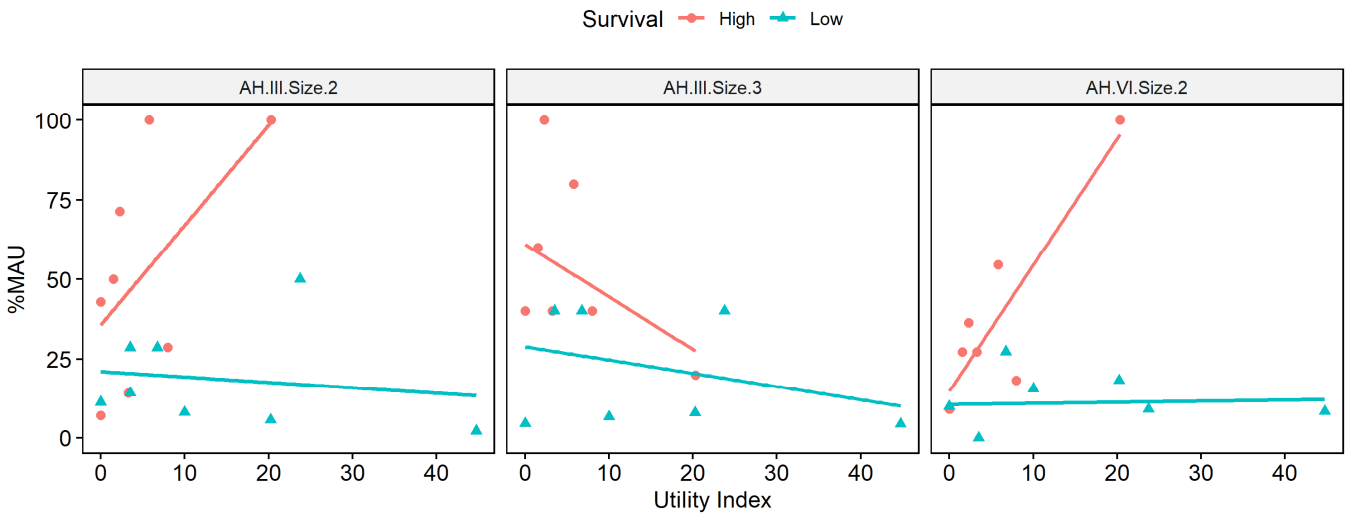

Figure 8 – %MAU plotted against utility indices: Standardized Food Utility Index for caprines (Size 2) and General Utility Index for equids (Size 3), distinguishing between high survival and low survival elements. See the Materials and Methods section for details.

Pairwise comparisons with utility indices

Survival	Set	Index	Spearman's rho	p-value
High	AH III Size 2	(S)FUI	0.826	0.011
High	AH III Size 3	GUI	-0.241	0.565
High	AH VI Size 2	(S)FUI	0.711	0.048
Low	AH III Size 2	(S)FUI	-0.315	0.409
Low	AH III Size 3	GUI	-0.23	0.584
Low	AH VI Size 2	(S)FUI	0.262	0.497

Table 9 – Pairwise comparisons between %MAU and nutritional utility, distinguishing between high survival and low survival elements. (S)FUI = Standardized Food Utility Index; GUI = General Utility Index.

4.2 Tooth wear analysis

As part of a pilot study, tooth mesowear and microwear analyses were performed on seven caprine teeth from AH III. The preservation is good, both at macroscopic and microscopic scales. Only one tooth was discarded from the mesowear analysis because it has broken cusps, and another one from the microwear analysis due to evidence of post-depositional alteration.

The mesowear score of 3.7 indicates moderately high levels of abrasion, i.e. similar to that of extant grazers (Table 10). In comparison to other extant Caprinae (genera *Ovis* and *Capra*), the sample from Aghitu-3 shows very high values suggesting a diet dominated by grasses all year around. The microwear pattern is

characterized by a high number of scratches (NS = 22.4), predominantly fine scratch widths (SWS = 0.33), moderate number of pits (NP = 14.5), predominantly large pits (%LP = 83.3%), and the absence of gouges, puncture pits, hypercoarse scratches and cross scratches.

	N	MWS	NP	NS	%LP	%G	SWS	%XS	%HC	%PP
Aghitu-3 AH III *Ovis/Capra*	7	3.7	14.5	22.4	83.3	0	0.33	0	0	0
C. caucasica	12	1.9	39.3	15.2	41.7	33.3	1.3	25	0	0
C. ibex	18	1.4	11.4	21.1	61.1	33.3	1.4	11.1	0	0
C. pyrenaica	11	1.3	22.5	18.3	36.4	18.2	1.3	18.2	0	0
O. ammon darwini	11	1.1	14.1	16.7	90.9	90.1	1.1	0	0	0
O. ammon poli	22	2.2	13.3	26.3	22.7	9.1	0.9	4.5	0	0

Table 10 – Summary of the mesowear and microwear data from Archaeological Horizon III of Aghitu-3 (this study, in gray) and extant Caprinae (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Rivals et al., 2010). N = Number of specimens; MWS = Mesowear score; NP = Average number of pits; NS = Average number of scratches; %LP = Percentage of individuals with large pits; %G = Percentage of individuals with gouges; SWS = Scratch width score; %XS = Percentage of individuals with cross scratches; %HC = Percentage of individuals with hypercoarse scratches; %PP = Percentage of individuals with puncture pits.

In comparison to extant wild ungulates, the sample from Aghitu-3 plots among the extant grazers (Figure 9). The microwear pattern is similar to that of the modern *Capra ibex* and significantly different from *C. pyrenaica* and *C. caucasica*. In comparison to modern *Ovis* species, the sample from Aghitu-3 has similar values for pits, but in terms of scratches it plots between the extant *Ovis ammon darwini* and *O. a. poli*. The diet of the Caprinae from Aghitu-3 was dominated by grasses. Trees or shrubs were not part of their diet, at least in the period preceding death.

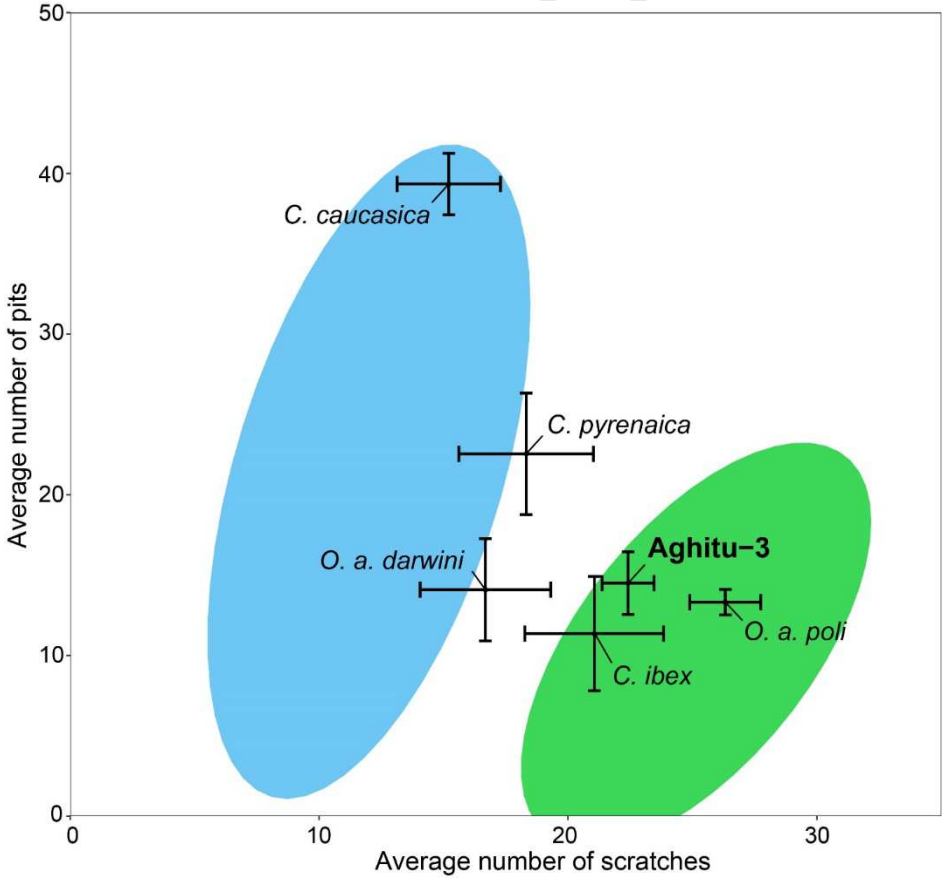

Figure 9 – Bivariate plot of the average numbers of pits and scratches for the samples from Archaeological Horizon III of Aghitu-3 and extant Caprinae. Error bars correspond to standard error of the mean (±1 SEM) for the fossil samples. Plain ellipses correspond

to the Gaussian confidence ellipses (p = 0.95) on the centroid for the extant leaf browsers (blue) and grazers (green) based on the reference database from Solounias and Semprebon (2002) and Rivals et al. (2010).

The variability of the microwear signal estimated on the number of scratches (standard deviation = 1.28; coefficient of variation = 0.06) is very low. These values permit to estimate the duration of accumulation of the caprine remains in the cave as well as the season of death. The low values suggest occupation of short duration of one season or less.

4.3 Avian fauna

The study of the avian fauna provides a synthesis of earlier finds (Kandel et al., 2017) and adds a number of unpublished remains found during further sorting and analysis. The sample now includes 332 Pleistocene bird bones, with 229 specimens identified to at least the order level. The majority of birds came from AHs III, VI and VII, and all layers were taxonomically dominated by small and medium sized perching birds (Passeriformes) (Table 11). Fourteen of the Passeriformes were further attributed to a more specific taxon. The rest of the bird remains belonged to the orders Galliformes, Anseriformes, Charadriiformes, Strigiformes, Apodiformes, Gruiformes and Falconiformes.

	AH III		**AH IV**		**AH V**		**AH VI**		**AH VII**	
	n	%	n	%	n	%	n	%	n	%
Perching bird (Passeriformes)	4	4%	-	-	1	9%	13	24%	9	6%
Perching bird - [approx. starling size] (Passeriformes)	4	4%	-	-	-	-	3	6%	8	5%
Perching bird - [approx. sparrow size] (Passeriformes)	37	37%	2	67%	8	73%	8	15%	36	22%
Perching bird - [approx. robin size] (Passeriformes)	22	22%	-	-	-	-	3	6%	6	4%
Finch? (cf. Fringillidae)	1	1%	-	-	-	-	-	-	4	2%
Swallow (Hirundinidae)	-	-	-	-	-	-	-	-	1	1%
Lark (Alaudidae)	-	-	-	-	-	-	-	-	1	1%
Lark? (cf. Alaudidae)	1	1%	-	-	-	-	1	2%	-	-
Eurasian skylark? (*Alauda* cf. *arvensis*)	-	-	-	-	1	9%	-	-	-	-
Raven (*Corvus corax*)	-	-	-	-	-	-	-	-	2	1%
Eurasian jay (*Garrulus glandarius*)	-	-	-	-	-	-	-	-	1	1%
Rook/Chough (*Corvus frugilegus*/*Pyrrhocorax pyrrhocorax*)	1	1%	-	-	-	-	-	-	-	-
Grey partridge (*Perdix perdix*)	-	-	-	-	-	-	-	-	1	1%
Chukar partridge (*Alectoris chukar*)	-	-	-	-	-	-	-	-	2	1%
Partridge (*Alectoris* sp.)	-	-	-	-	-	-	-	-	1	1%
Partridge *(Alectoris* sp./*Perdix* sp.)	-	-	-	-	-	-	1	2%	2	1%
Gamefowl [approx. partridge size] (Galliformes)	2	2%	-	-	-	-	-	-	1	1%
Gamefowl [approx. pheasant size] (Galliformes)	2	2%	-	-	-	-	1	2%	3	2%
Diving duck (*Aythya* sp.)	-	-	-	-	-	-	-	-	1	1%
Tufted duck? (*Aythya* cf. *fuligula*)	-	-	-	-	-	-	-	-	1	1%
Teal (*Anas crecca*)	-	-	-	-	-	-	1	2%	1	1%
Mallard (*Anas platyrhynchos*)	-	-	-	-	-	-	-	-	1	1%

Mallard? (*Anas* cf. *platyrhynchos)*	-	-	-	-	-	-	-	-	2	1%
Shelduck? (Anatidae cf. *Tadorna* sp.)	-	-	-	-	-	-	-	-	1	1%
Duck (Anatidae)	-	-	-	-	-	-	-	-	2	1%
Marsh harrier (C*ircus aeruginosus*)	-	-	-	-	-	-	-	-	1	1%
Raptor [approx. buzzard size] (Accipitridae)	-	-	-	-	-	-	-	-	1	1%
Spotted crake (*Porzana porzana*)	-	-	-	-	-	-	-	-	1	1%
Wader (Scolopacidae/Charadriidae)	-	-	-	-	-	-	1	2%	9	6%
Snipe? (Scolopacidae cf. *Galinago* sp.)	-	-	-	-	-	-	2	4%	4	2%
Eared owl (*Asio* cf. *flammeus*)	-	-	-	-	-	-	1	2%	-	-
Common swift (*Apus apus*)	-	-	-	-	-	-	5	9%	-	-
Aves indet.	27	27%	1	33%	1	9%	14	26%	60	37%
Total:	101	100%	3	100%	11	100%	54	100%	163	100%

Table 11 – Identification of bird bones from Archaeological Horizons VII–III of Aghitu-3.

No direct evidence of human modification was found on any of the bird bones. Although comparisons of the relative abundance of skeletal elements should be interpreted with caution (Laroulandie, 2000), an earlier analysis of the skeletal distribution of the bird remains at Aghitu-3 has indicated a predominance of wing bones in AHs III, VI and VII, while elements of the cranium, shoulder girdle and axial skeleton were underrepresented (Kandel et al., 2017). Such a pattern of predominantly unfragmented wing bones has been observed in taphonomic studies of prey remains of certain birds of prey (Ericson, 1987; Laroulandie, 2002). Therefore, together with the absence of anthropogenic modifications, the skeletal element representation suggests that an avian predator accumulated the bird remains. This may explain the presence of Anatidae, Alaudidae, Phasianidae and Charadriidae/Scolopacidae that are usually not associated with caves but are commonly caught by owls and raptors. A possible accumulator is the (short?) eared owl (*Asio* cf. *flammeus*) attested at the site. The species of the genus *Asio* are known to feed regularly on small perching birds (Sekour et al., 2010). However, this genus is unlikely to explain the presence of larger bird species such as ducks, larger corvids and fowl. For these species a mammalian accumulator is also possible. Finally, some species such as common swift (*Apus apus*), swallow (Hirundinidae) and perhaps raven (*Corvus corax*) could have nested within protected areas of the cave walls and ceiling (Kandel et al., 2017).

5 Discussion

5.1 Large mammals and tooth wear analysis

The zooarchaeological study of Aghitu-3 confirms previous paleoenvironmental reconstructions inferring mild and relatively humid conditions during the formation of AH VI and a more dry and open landscape during the formation of AH III. For AH III, tooth mesowear and microwear are supporting this result. The high abrasiveness of the diet of the Caprinae are indicative of grazing, suggesting that these animals lived in open habitats. The subsistence strategies of Upper Paleolithic foragers at Aghitu-3 are overall consistent with those attested at sites in the southern Caucasus, namely seasonal occupations and a focus on adult medium and large ungulates. The zooarchaeological assemblage of Aghitu-3 differs from Paleolithic assemblages in the Caucasus region in that equid, rather than bison/aurochs, is the second most abundant taxon.

Most researchers have identified archaeological caprines from the southern Caucasus as Caucasian tur (*Capra caucasica*; e.g. Bar-Oz and Adler, 2005; Yeshurun et al., 2014). In this study we have decided to leave the identification at the genus level, but note that at the cave site of Karin Tak, less than 100 km east of

Aghitu-3, morphologically unidentified remains dating to MIS 3 and 2 have been assigned to *Capra aegagrus* by aDNA metabarcoding (Antonosyan et al., 2019). Fossils from the same deposits have been similarly assigned to *Ovis sp.* (Antonosyan et al., 2019). Wild sheep is not attested in the Paleolithic deposits at Aghitu-3, but is present in the younger Epigravettian faunal assemblage from Kalavan-1 (Bălăşescu et al., 2017). We also assigned wild cattle remains from Aghitu-3 to *Bos*/*Bison*, as no specimen was identifiable at higher taxonomic resolution. However, is worth noting that the two taxa potentially had very different ecological preferences. Other researchers have recognized both species in their assemblages (Bar-Oz et al., 2008), while at Karin Tak, aDNA metabarcoding did not resolve the identification beyond the tribe Bovini (Antonosyan et al., 2019).

Most of the assemblage was fragmented while it still held nutritional value and did not suffer intense post-depositional breakage or weathering. The relative proportions of percussion and tooth marks indicate that the large mammals were mainly accumulated through human agency, although mammalian carnivores independently deposited a small quantity of bones. Based on the size of the tooth marks, we suggest that large canids were active at the site during the formation of AH VI, whereas small canids or medium felids contributed to AH III. Density-mediated attrition of the assemblage was mild at most. A variety of butchery activities are attested and there is limited cut mark evidence that equid and caprine carcasses may have been processed differently. In the future, larger fossil samples may allow to elaborate this hypothesis further.

The association of skeletal element representation and food utility indicates that medium sized (caprine) carcasses were selectively transported to Aghitu-3 to maximize return rates. This may have been the case for large (equid) carcasses as well, but the possible defleshing of the femur prior to transport would have obscured this pattern. These strategies are apparently inconsistent with those reported for other sites in the region. Bar-Oz and Adler (2005) note the lack of correlation between food utility and %MAU for Caucasian tur in the late Middle Paleolithic layers 6 and 7 at Ortvale Klde. They interpret this as absence of evidence for selective transport and note that "…*the net nutritional gains must have out-weighed transport costs*" (Bar-Oz and Adler, 2005: 204). Similarly, Bar-Oz et al. (2008) do not find quantitative support for selective transport of tur and bison in the pooled Upper Paleolithic assemblage at Dzudzuana, although the authors subsequently suggest that extensive field butchery may have occurred nevertheless (Bar-Oz et al., 2008: 143). Finally, Yeshurun et al. (2014) suggest that during the Upper Paleolithic entire medium carcasses were transported to Bondi Cave, while large carcasses were selectively transported. However, they do not test this hypothesis statistically. Thus, a different carcass transport strategy has been inferred for each site.

Our study of Aghitu-3 is not directly comparable with those of Ortvale Klde and Dzudzuana for two reasons. First, Bar-Oz and colleagues (Bar-Oz and Adler, 2005; Bar-Oz et al., 2008) used a different utility index compared to us. Second, and most importantly, the authors test all elements together for correlation with food utility, despite evidence for density-mediated attrition in the deposits. As discussed in the Materials and Methods section, there is conceptual and empirical support for the practice of considering low- and high-density elements separately in this type of analysis (Marean and Frey, 1997; Marean and Cleghorn, 2003; Yeshurun et al., 2007; Schoville and Otárola-Castillo, 2014; Faith and Thompson, 2018). To allow for comparison we recalculated %MAU from the raw data published for Ortvale Klde, Dzudzuana and Bondi (Bar-Oz and Adler, 2005; Bar-Oz et al., 2008; Yeshurun et al., 2014) and tested for correlation with the Standardized Food Utility Index (Figure 10, Table 12).

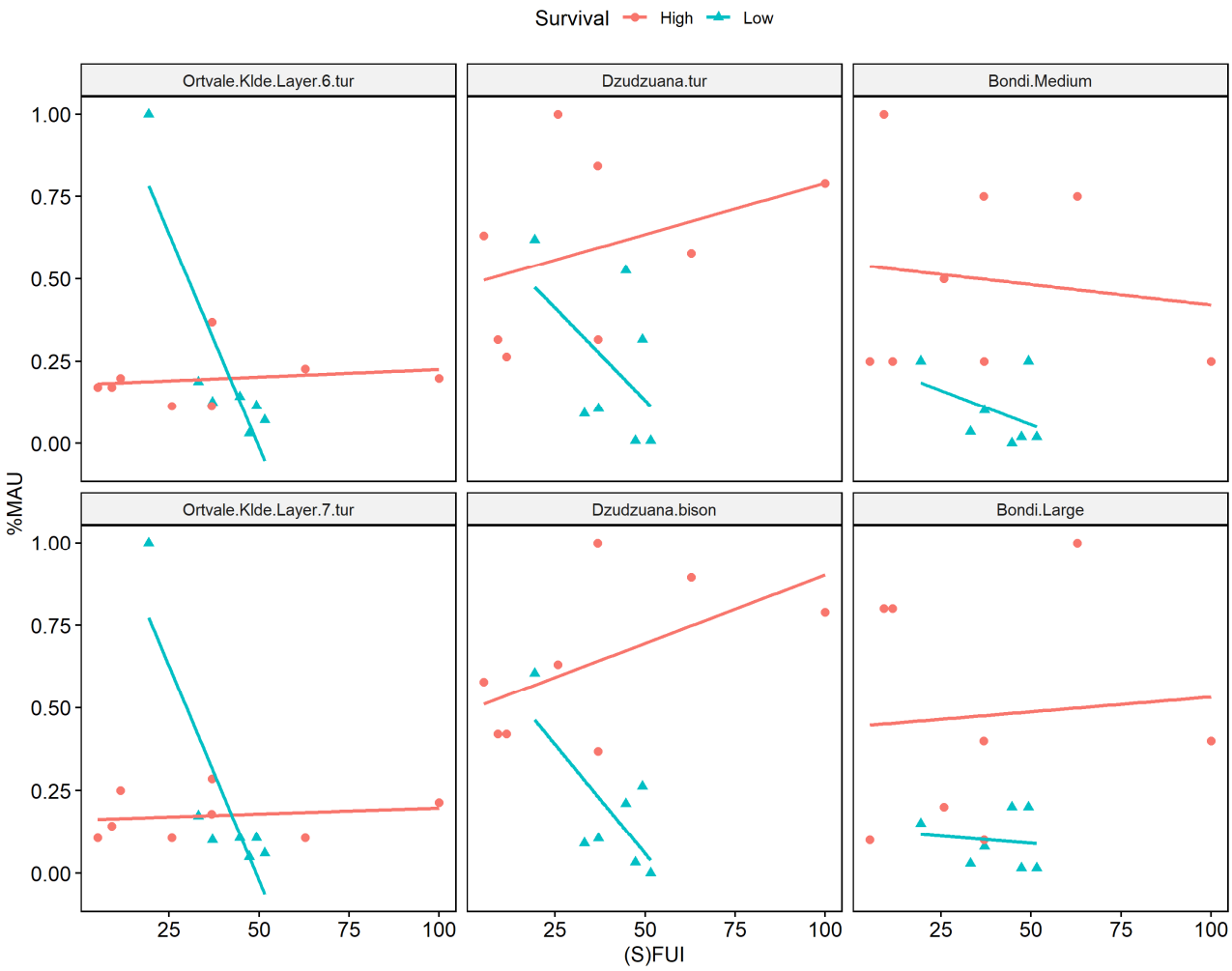

Figure 10 – %MAU of ungulates from Ortvale Klde (late Middle Paleolithic), Dzudzuana and Bondi Cave (both Upper Paleolithic) plotted against the Standardized Food Utility Index. Data from Bar-Oz and Adler (2005), Bar-Oz et al. (2008) and Yeshurun et al. (2014). See the Materials and Methods section for details.

Pairwise comparisons with utility indices

Survival	Set	Spearman's rho	p-value
High	Ortvale Klde MP Layer 6 tur	0.473	0.237
High	Ortvale Klde MP Layer 7 tur	0.293	0.482
High	Dzudzuana UP tur	0.216	0.608
High	Dzudzuana UP bison	0.419	0.301
High	Bondi UP medium	-0.077	0.857
High	Bondi UP large	0.182	0.666
Low	Ortvale Klde MP Layer 6 tur	-0.857	0.014
Low	Ortvale Klde MP Layer 7 tur	-0.721	0.068
Low	Dzudzuana UP tur	-0.541	0.210
Low	Dzudzuana UP bison	-0.500	0.253
Low	Bondi UP medium	-0.346	0.448
Low	Bondi UP large	-0.218	0.638

Table 12 – Pairwise comparisons between %MAU and nutritional utility (Standardized Food Utility Index), distinguishing between high survival and low survival elements.

All of the correlations between low survival element representation and food utility are negative and mostly insignificant, as they track density-mediated attrition (Faith and Thompson, 2018). The correlations

between high survival element representation and food utility are statistically insignificant. This supports Bar-Oz and Adler's (2005) conclusion that tur carcasses were not selectively transported to Ortvale Klde. Bar-Oz et al.'s (2008) lack of quantitative support for selective transport at Dzudzuana is also replicated by our results. Finally, we provide quantitative evidence that neither medium nor large carcasses were selectively transported to Bondi Cave. All sites considered are interpreted as seasonal hunting camps, probably occupied at times when ungulate herds were migrating from the winter to the summer pastures and vice versa. Here we assume that Neanderthals and AMH were equally capable of making rational decisions based on transport costs. Therefore, we interpret the pattern of selective transport at Aghitu-3 as a suggestion that foragers at this site were exploiting a larger territory and transporting carcasses for longer distances compared to the foragers of Ortvale Klde, Dzudzuana and Bondi Cave.

Tooth microwear (for AH III) confirms the recurrent hunting of caprines related to occupation of the cave that always occurred during the same season. With regard to the ecological preferences of extant caprines in the region (Nowak, 1999; Weinberg, 2002; Baskin and Danell, 2003), in spring and summer their diet is dominated by grass, which is rich in phytoliths and highly abrasive. Evidence for a diet based mainly on grass would be reflected by a high number of scratches in the microwear pattern. Conversely, in fall and winter their diet is based mainly on browse (dicots, leaves from shrubs and trees), which is significantly less abrasive than grass. Consequently, a microwear pattern with low numbers of scratches would be expected if the animals died during the cold season. The sample from AH III, with its high number of scratches, suggests a highly abrasive grazing diet. Therefore, we conclude that these animals were most likely hunted in spring or summer.

5.2 Avian fauna

Although all bird species found in Aghitu-3 are currently present in Armenia (Kandel et al., 2017), certain taxa such as *Anas crecca,* Anatidae cf. *Tadorna* sp., *Aythya* cf. *fuligula* and *Porzana porzana* are today mainly passage migrants or winter visitors (Adamian and Klem, 1997). It is unclear whether this was also the case during the late Pleistocene. In AH V and AH IV, sample sizes were too small to make any paleoecological inferences. AH III was richer in bird remains, but the absence of diagnostic elements hampered species identification and therefore also paleoenvironmental reconstruction. The samples from AH VII and AH VI provided more insight into the conditions around the site.

The presence of at least two species of partridge (*Alectoris chukar* and *Perdix perdix*) indicates the existence of relatively open environments. While the grey partridge (*Perdix perdix*) has a certain tolerance for colder and more humid conditions (Meriggi et al., 1991), the Chukar partridge (*Alectoris chukar*) is restricted to regions with a warmer climate and has a preference for dry, rocky outcrops with some shrub vegetation (Stuart Baker, 1922; Watson, 1962; Awan et al., 2006). This is further corroborated by the occurrence of larks (Alaudidae) and a possible Eurasian skylark (*Alauda* cf. *arvensis*), suggesting a fairly open landscape (Kuiper et al., 2013). Furthermore, open conditions are indicated by the possible presence of the short-eared owl (*Asio* cf. *flammeus*), a species of scrubland, moorland and other open environments (Svensson and Grant, 1999). The specimen from Aghitu-3 could not, however, be confidently distinguished from its close relative, the long-eared owl (*Asio otus*), which is associated with a more closed vegetation (Svensson and Grant, 1999). A somewhat anomalous find was a fragment of a Eurasian jay (*Garrulus glandarius*), a bird with a preference for old trees (Svensson and Grant, 1999). This could indicate the presence of at least some trees or larger shrubs in the vicinity of the site, such as in riparian zones seen today along the Vorotan River.

The bones of a number of duck species (*Anas crecca*, *A. platyrhynchos*, *Aythya* sp*., Aythya* cf. *fuligula* and cf. T*adorna* sp.), a spotted crake (*Porzana porzana*), a number of small waders (Scolopacidae/Charadriidae and Scolopacidae cf. *Gallinago* sp.) and a marsh harrier (*Circus aeruginosus*) suggest the presence of

shallow fresh water in the proximity of the site (Svensson and Grant, 1999). Particularly, the marsh harrier is known to be associated with wetlands, especially reed beds, and generally avoids closed woodland (Takácsová, 2007).

In summary, the bird remains from Aghitu-3 (at least for AH VII and AH VI) indicate a temperate, open environment with some larger shrubs in proximity to a freshwater reservoir with riparian vegetation. This might be the Vorotan River or one of its tributaries (Kandel et al., 2017). No clear differences were observed between AH VII and AH VI. This reconstruction is consistent with the presence in AH VII of the mole vole (*Ellobius lutescens*) and abundant Brandt's hamster (*Mesocricetus brandti*), which suggest near-modern conditions (Kandel et al., 2017). Due to small sample sizes, the other layers did not allow for diachronic comparisons.

6 Conclusion

The analyses presented in this paper support and refine previous paleoenvironmental reconstructions of the Late Pleistocene landscapes of the Syunik highlands of southern Armenia. The hunting preferences of the Upper Paleolithic foragers at Aghitu-3 are consistent with those inferred for Middle and Upper Paleolithic foragers inhabiting sites in the southern Caucasus, namely a focus on adult medium and large ungulates during short and repeated seasonal occupations. Nevertheless, selective transport of medium sized carcasses suggests that the foragers of Aghitu-3 hunted in a larger territory compared to other groups in the region. The accumulation of bird remains does not appear to be directly related to human activity in the cave. While some species may have nested in the cave, raptors and carnivores were likely accumulators as well. The avian fauna indicates a temperate, open environment with presumably some larger shrubs in proximity to a freshwater reservoir with riparian vegetation. Finally, tooth wear analyses support the applicability of this approach to infer seasonality of occupation at short-term hunting camps in the region, with evidence provided for spring or summer occupations. Further research remains necessary to detect possible diachronic trends in carcass transport strategies, the impact of prey body size on butchery routines and the changing structure and contribution of the carnivore guild to the formation of Paleolithic faunal assemblages in the region.

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: